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Long-term changes of collembolan communities in
forest soils

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ABSTRACT. Soil collembolan communities were studied in old-growth western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) forests and a young Douglas-fir plantation on southern Vancouver Island, British Columbia, Canada. Coenotical data of collembolan communities were analysed to establish the changes that occurred during the intervening 17 and 19 years. Ordination and cluster analysis (Euclidean distance - Ward's method) were used to compare the data from each locality and different collecting dates.

Species number (S), evenness (E) and Shannon-Wiener index of diversity (H') decreased in the old-growth Douglas-fir stand between 1974 and 1991, whereas in the old-growth western hemlock stand species number increased, evenness decreased slightly and H' was almost the same in 1974 and 1991. These parameters increased substantially in the young Douglas-fir plantation between 1973 and 1992. Ordination analysis put the data from the old-growth stands close together, whereas they were widely separated in the young plantation. Also the cluster analysis showed great faunistic identity. Ordination analysis of Log₁₀ x+1 transformed data also showed good time separation for the young plantation. Only medium changes in the faunistic composition were noted for the old-growth stands. Dominant species changed slightly in the western hemlock, but changed more drastically in the Douglas-fir stand during the 17 years. Changes in the climax sites were probably caused by air-borne pollutants.

INTRODUCTION

During the last few decades, international ecological communities have concentrated on environmental problems of regional and global scales. Scientists have been trying to separate and analyse long-term

changes of ecological parameters caused by human activity from their normal oscillation patterns. The most important contemporary scientific activities concerning long-term changes of the global scale have been concentrated in the IGBP (International Geosphere-Biosphere Programme).

Most studies of long-term changes have been performed by plant ecologists on vegetation cover. Single ecosystem parameters exhibit different reactions to environmental changes. Some of these parameters may react earlier than the plants, others may respond with a delay. Soil fauna is an important component of each terrestrial ecosystem. It comprises different ecomorphological groups that may show an intimate or a loose relationship to the soil. *Collembola* are an ecomorphologically well diversified unit of the soil mesofauna (RUSEK 1989); they reach high densities in almost all ecosystem and are rich in species. Therefore, they are very suitable for ecological field studies. It is surprising that only few data have been published about long-term changes of collembolan communities influenced by different environmental stressors. DUNGER's (1991) contribution dealt with long-term changes of soil fauna (including *Collembola*) in forest stands influenced by air-borne pollutants. His observations were based on faunistic data and he did not evaluate the quantitative aspects of the community structure. He concluded that the faunistic composition of *Collembola* did not change under the pollutants' impact. Since 1959, *Collembola* and other ecosystem parameters have been measured in the Tatra National Park, Slovakia, and collembolan communities have shown high sensitivity to long-distance transported acid deposits (RUSEK 1993).

Recently, we have had the opportunity to repeat soil sampling on three permanent forest plots on Vancouver Island where the collembolan communities were studied in 1973 and 1974. In this contribution, we analyse collembolan communities from these plots and describe their changes after 17 and 19 years.

MATERIAL AND METHODS

Ten (or 9) soil cores (5 cm in diameter, 10 cm deep) were collected at each sampling date in each site and transported in plastic bags to the laboratory. *Collembola* were extracted using high-gradient extractors. The sorted material was determined to species and counted. From each set of samples the basic community parameters were calculated, e.g. density in 10 samples (A), dominance (D) and constancy (C), characteristic species composition (= spp. with C \geq 50%), species number

(S), evenness (E) and Shannon-Wiener index of diversity (H'). Ordination and cluster analysis (Euclidean distance - Ward's method) were used to compare the data from each site and different collecting dates (McCUNE 1987, RUSEK 1984, TER BRAAK 1987).

SITE DESCRIPTION

Soil collembolan communities were studied in old-growth western hemlock [*Tsuga heterophylla* (RAF.) SARG.] and Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] forests and a young Douglas-fir plantation on southern Vancouver Island, British Columbia, Canada.

Site 1. Old-growth western hemlock forest at China Beach Provincial Park on the western coast of Vancouver Island (48°26'N, 124°06'W), 50 m above sea level. Climax forest stand about 250 to 300-year-old, with major understory species: western hemlock, huckleberry (*Vaccinium parvifolium* SMITH), bracken fern [*Pteridium aquilinum* (L.) KUHN] and mosses (*Musci* spp.). Soil type: Pseudogley (KUBIENA 1953). The sampling dates compared were: 24 IX 1974 and 7 V 1991.

Site 2. Old-growth Douglas-fir forest at Thomas S. Francis Provincial Park, Saanich Peninsula on Vancouver Island (48°29'N, 123°27'W), 110 m above sea level, climax forest stand about 300-year-old with snowberry [*Symphoricarpos albus* (L.) BLAKE] and mosses (*Musci* spp.) as dominant understory plants. Soil type: Eutrophic Braunerde (KUBIENA 1953). The sampling dates compared were: 21 X 1974, 8 I 1975 and 6 V 1991.

Site 3. Douglas-fir plantation at the Shawnigan Lake Fertilizer Installation (48°39'N, 123°41'W), about 320 m above sea level. The stand was 25 years old when the first samples were taken in 1973 in the ToFo (control) plots. The major understory species were: salal (*Gaultheria shallon* PURSH), bracken fern and Oregon grape [*Mahonia nervosa* (PURSH) NUTT.]. Soil type: Oligotrophic Braunerde (KUBIENA 1953). The sampling dates compared were: 2 XI 1973 and 27 X 1992.

RESULTS

A total of 119 species of *Collembola* were established in all three sites (Table 1), 39 in the western hemlock site (Site 1), 38 in the climax Douglas-fir forest (Site 2) and 75 in the Douglas-fir plantation (Site 3).

Table 1

Collembolan density (A) and constancy (C) in soil samples from western hemlock (1), Douglas-fir climax (2) and Douglas-fir plantation (3) taken in 1973-1975 and 1991-1992.

Site No. Sampling year Density and constancy	1				2				3					
	1974		1991		1974		1975		1991		1973		1992	
	A	C	A	C	A	C	A	C	A	C	A	C	A	C
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Hymenaphorura similis</i> (FOLSOM, 1917)	527	100	866	100	-	-	-	-	-	-	-	-	-	-
<i>Mesaphorura yosii</i> (RUSEK, 1967)	162	100	535	100	26	80	64	90	43	60	342	89	157	89
<i>Sensiphorura marshalli</i> RUSEK, 1976	154	100	398	100	-	-	-	-	-	-	-	-	1	11
<i>Tomolonus reductus</i> MILLS, 1949	151	100	58	100	-	-	-	-	-	-	-	-	-	-
<i>Folsomia ozeana yosii</i> , 1954	147	89	176	100	-	-	-	-	-	-	-	-	-	-
<i>Megalothorax minimus</i> WILLEM, 1902	79	89	79	90	52	60	339	100	31	60	15	78	15	33
<i>Cyclograna horrida</i> (YOSHI , 1960)	52	89	1	10	15	60	4	30	3	30	-	-	9	44
<i>Parisotoma notabilis</i> (SCHÄFFER, 1896)	34	78	30	80	74	80	41	70	12	40	-	-	-	-
<i>Chaetophorura vancouverica</i> RUS., 1967	38	67	13	70	-	-	-	-	-	-	-	-	-	-
<i>Sinella binoculata</i> (SCHÖTT, 1896)	23	67	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paranura colorata</i> MILLS, 1934	19	67	-	-	1	10	-	-	-	-	-	-	1	11
<i>Onychiurus eisi</i> RUSEK, 1976	12	67	82	80	-	-	-	-	-	-	-	-	-	-
<i>Micrisotoma achromata</i> BELLINGER, 1952	48	55	153	100	-	-	-	-	1	10	-	-	-	-
<i>Pogonognathellus elongatus</i> MAYN., 1951	20	55	10	60	-	-	-	-	-	-	-	-	-	-
<i>Christobella setosa</i> (CANBY, 1926)	9	55	4	30	-	-	-	-	-	-	3	11	-	-
<i>Arrhopalites</i> sp.	8	55	16	60	-	-	-	-	-	-	-	-	-	-
<i>Sphaeridia</i> sp.n.	4	33	3	20	34	60	8	60	-	-	-	-	-	-
<i>Isotomidae</i> juv.	15	22	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oncopodura</i> sp.	4	22	1	10	-	-	-	-	-	-	-	-	-	-
<i>Ceratophysella</i> sp.	3	22	6	30	-	-	-	-	-	-	-	-	-	-
<i>Odontella cornifer</i> MILLS, 1934	4	11	1	10	4	10	51	40	1	10	-	-	-	-
<i>Willemia denisi</i> MILLS, 1932	1	11	2	20	15	50	-	-	11	70	-	-	5	44
<i>Pseudisotoma sensibilis</i> (TULLBERG, 1876)	-	-	256	100	96	40	51	80	18	50	-	-	-	-
<i>Folsomia macroseta</i> FORD, 1962	-	-	66	70	-	-	-	-	-	-	-	-	-	-

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Vertagopus</i> sp.	-	-	48	70	-	-	-	-	-	-	-	-	-	-
<i>Cyclograna krafti</i> (SCOTT, 1962)	-	-	28	60	-	-	-	-	-	-	-	-	1	11
<i>Lophognathella choreutes</i> (BÖRNER, 1908)	-	-	10	50	-	-	-	-	-	-	-	-	1	11
<i>Xenylla humicola</i> (O. FABRIC., 1780)	-	-	18	40	25	90	8	40	910	70	1	11	-	-
<i>Lepidocyrtus lanuginosus</i> (GMELIN, 1788)	-	-	10	40	-	-	-	-	-	-	-	-	-	-
<i>Deutonura</i> sp.	-	-	4	30	-	-	-	-	-	-	-	-	-	-
<i>Folsomia bisetosa</i> GISIN, 1953	-	-	10	20	-	-	-	-	-	-	-	-	-	-
<i>Tetracanthella pacifica</i> RUS. & MARS., 1976	-	-	3	20	-	-	-	-	-	-	-	-	-	-
<i>Friesia fara</i> CH. & B., 1973	-	-	2	20	-	-	-	-	-	-	-	-	-	-
<i>Pseudanurophorus</i> sp.	-	-	2	10	-	-	-	-	-	-	-	-	-	-
<i>Entomobrya triangularis</i> SCHÖTT, 1896	-	-	2	10	9	50	1	10	17	60	-	-	-	-
<i>Odontella biloba</i> C. & B., 1980	-	-	1	10	-	-	-	-	-	-	4	11	-	-
<i>Isotoma</i> sp.	-	-	1	10	-	-	-	-	-	-	-	-	-	-
<i>Ptenothrix maculosa</i> (SCHÖTT, 1891)	-	-	1	10	-	-	-	-	-	-	2	22	3	22
<i>Friesia pentacantha</i> MILLS, 1934	-	-	1	10	-	-	-	-	-	-	-	-	-	-
<i>Cryptopygus</i> sp. n.	-	-	-	-	172	100	26	60	28	50	-	-	-	-
<i>Sinella</i> sp. n.	-	-	-	-	25	100	23	60	-	-	-	-	-	-
<i>Hymenaphorura cocklei</i> (FOLSOM, 1908)	-	-	-	-	80	90	24	90	40	80	-	-	21	56
<i>Granuliphorura obtusochaeta</i> RUS., 1976	-	-	-	-	19	80	4	20	-	-	-	-	-	-
<i>Tomocerus vulgaris</i> (TULLBERG, 1871)	-	-	-	-	14	70	4	20	8	40	-	-	-	-
<i>Mesaphorura macrochaeta</i> RUSEK, 1967	-	-	-	-	65	60	104	30	62	50	-	-	7	11
<i>Isotoma</i> sp.2	-	-	-	-	59	60	11	50	10	50	-	-	-	-
<i>Mesaphorura pacifica</i> RUSEK, 1976	-	-	-	-	37	60	12	60	6	30	11	22	-	-
<i>Ptenothrix</i> sp.	-	-	-	-	12	50	10	70	2	20	-	-	-	-
<i>Mesaphorura krausbaueri</i> BÖRNER, 1901	-	-	-	-	5	40	1	10	-	-	-	-	-	-
<i>Mesaphorura ruseki</i> C. & B., 1980	-	-	-	-	120	30	6	10	190	70	-	-	5	11
<i>Arrhopalites hirtus</i> CHRISTIANSEN, 1966	-	-	-	-	6	30	6	40	-	-	-	-	-	-
<i>Multivesicula columbica</i> RUSEK, 1982	-	-	-	-	4	10	6	40	-	-	-	-	-	-
<i>Morulodes serratus</i> (FOLSOM, 1916)	-	-	-	-	1	10	1	10	8	50	4	22	-	-
<i>Willemia scandinaviica</i> STACH, 1949	-	-	-	-	1	10	9	20	20	20	-	-	-	-
<i>Christobella ornata</i> (FOLSOM, 1902)	-	-	-	-	1	10	-	-	1	10	-	-	4	22

The characteristic species composition in site 1 comprised *Hymenaphorura similis*, *Mesaphorura yosii*, *Sensiphorura marshalli*, *Tomolonus reductus*, *Folsomia ozeana*, *Megalothorax minimus*, *Cyclograna horrida*, *Parisotoma notabilis*, *Chaetophorura vancouverica*, *Sinella binoculata*, *Paranura colorata*, *Onychiurus eisi*, *Micrisotoma achromata*, *Pogonognathellus elongatus*, *Christobella setosa* and *Arrhopalites* sp. in the 1974 samples. To these were added *Pseudisotoma sensibilis*, *Folsomia macroseta*, *Vertagopus* sp., *Cyclograna krafti* and *Lophognathella choreutes* in 1991. However, *C. horrida*, *S. binoculata*, *P. colorata* and *Ch. setosa* from the former list became rare or extinct.

In the 1974-75 samples, Site 2 contained the following characteristic species composition: *Cryptopygus* sp.n., *Sinella* sp.n., *Hymenaphorura cocklei*, *Xenylla humicola*, *Mesaphorura yosii*, *Parisotoma notabilis*, *Granuliphorura obtusochaeta*, *Pseudisotoma sensibilis*, *Tomocerus vulgaris*, *Ptenothrix* sp., *Mesaphorura macrochaeta*, *Isotoma* sp.2, *Megalothorax minimus*, *Mesaphorura pacifica*, *Sminthurinus* sp., *Sphaeridia* sp.n., *Cyclograna horrida*, *Willemia denisi* and *Entomobrya triangularis*. Additions from the 1991 samples were *Lepidocyrtus* sp., *Mesaphorura ruseki*, *Onychiurus flavescens*, but the following 8 species became rare or extinct: *C. horrida*, *P. notabilis*, *Sphaeridia* sp.n., *Sinella* sp.n., *G. obtusochaeta*, *M. pacifica*, *Ptenothrix* sp. and *Sminthurinus* sp.

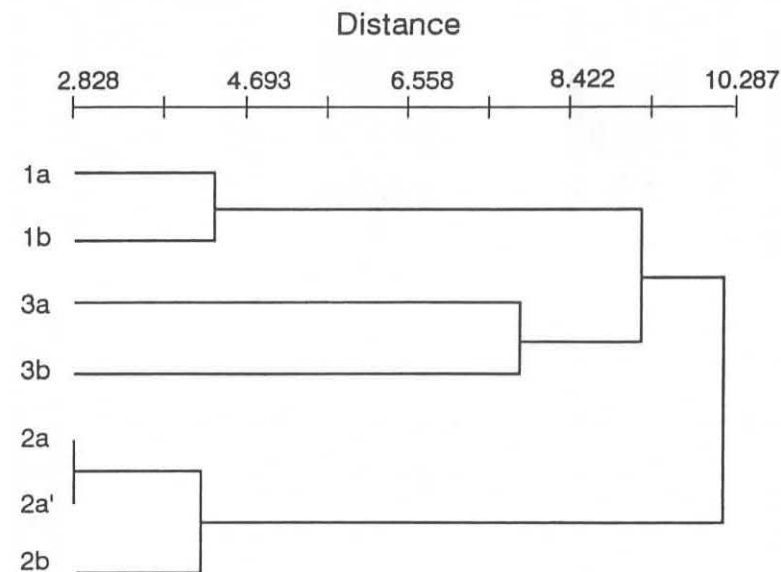
Site 3 samples in 1973 contained the following characteristic species composition: *Mesaphorura yosii*, *Megalothorax minimus* and *Onychiurus flavescens*. In 1992, the characteristic species group in Site 3 was only *Mesaphorura yosii* and *Hymenaphorura cocklei*.

During the two decades, the species number increased from 22 to 36 and from 33 to 54 in site 1 and 3, respectively, but decreased from 30 to 25 on site 2 (Table 2). The species diversity was high and did not change over time in site 1. It increased substantially in site 3 and decreased from a high to a substantially lower value in site 2 (Table

Table 2
Species number (S), diversity (H'), and evenness (E) in soil samples from western hemlock climax (1), Douglas-fir climax (2), and Douglas-fir plantation (3) taken in 1973-1975 and 1991-1992

Site	1		2		3		
Year	1974	1991	1974	1975	1991	1973	1992
S	22	36	30	28	25	33	54
H'	2.234	2.257	2.742	2.292	1.694	2.120	2.860
E	0.723	0.630	0.806	0.688	0.526	0.606	0.717

2). The evenness was very high in site 2 and decreased there over time to the lowest value. An increase of E-value was observed in site 3; it decreased in site 1 (Table 2).

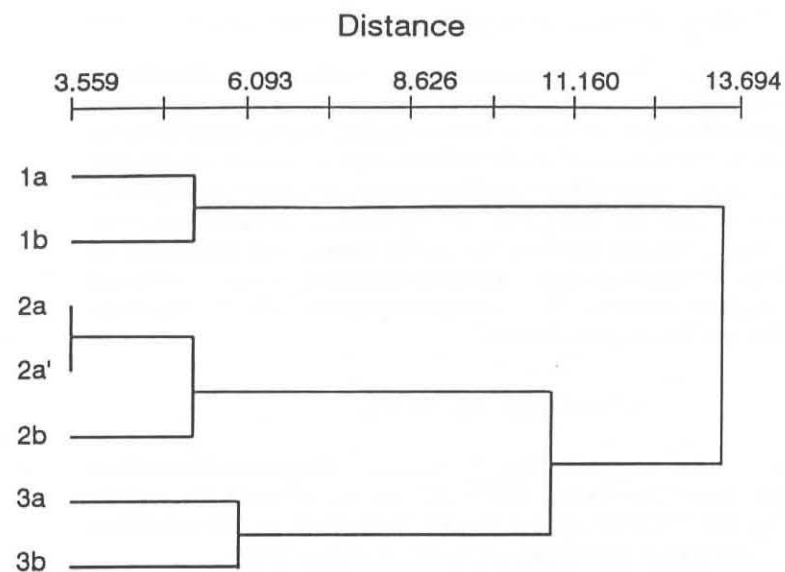
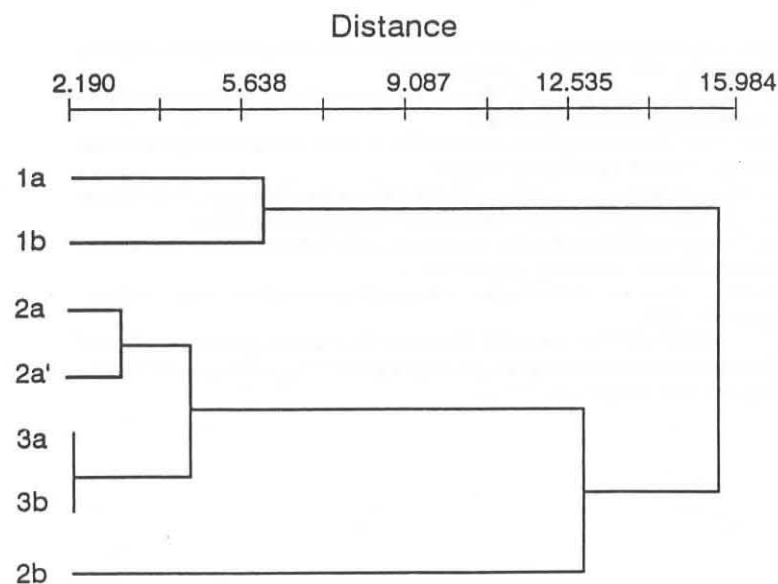


1. Faunistic cluster analysis of presence - absence (0,1) data

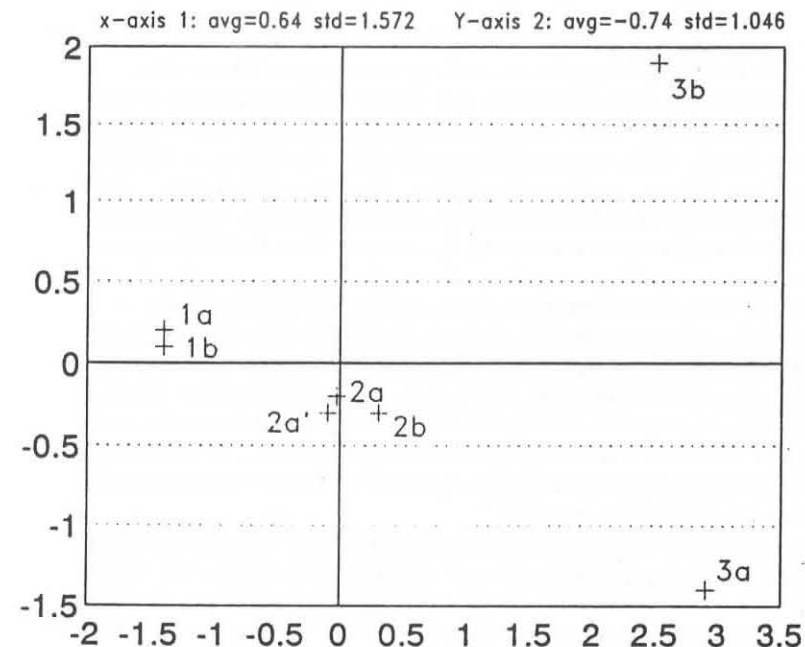
The cluster analysis of presence-absence (0,1) data showed high faunistic divergence among all three sites and between 1973 and 1992 samples from site 3. There was also high similarity over time in site 2 and site 1 (Fig. 1). The 1974 and 1975 samples from site 2 were faunistically almost identical.

The cluster analysis of $\log_{10}x+1$ transformed input data showed high coenotical dissimilarity among all three sites (Fig. 2). The 1974 and 1975 samples were coenotically almost identical in site 2, the difference over time between earlier and recent samples was the same in site 1 and 2 and little more expressive in site 3.

The cluster analyses of non-transformed abundance data showed high dissimilarity in the dominant species composition among site 1, recent samples from site 2 and site 3 together with the earlier samples from site 2 (Fig. 3). The dominant species were almost identical over time in site 3, less similar between 1974 and 1975 samples in site 2 and more diversified in site 1 (Fig. 3).

2. Coenotical cluster analysis of $\text{Log}_{10}x+1$ transformed data

3. Functional cluster analysis of non-transformed abundance data



4. Ordination analysis

The ordination analysis (Fig. 4) showed clear difference among all sites and high identity of collembolan communities over time in sites 1 and 2, whereas they were quite different in site 3.

DISCUSSION

Two of the three sites studied were climax ecosystems and the third one a 15 years old plantation at the beginning of our investigation. The composition and parameters of the collembolan communities reflected well the developmental age of the sites. The species number in the climax stands was high and rich in constant and euconstant forms (characteristic species composition), whereas in the young Douglas-fir plantation it was also high and had even increased over time to extremely high numbers, but it still contained only 3 or 2 euconstant and constant species. The parameters on site 3 were characteristic for developing communities of disturbed ecosystems.

As site 3 recovered to the former climax forest status, new collembolan species were entering during the secondary succession. Even after 44 years of plantation growth, it had not yet established a well developed collembolan community. The extensive long-term changes were related to succession there. The faunistic composition, as well as coenotic parameters in the climax communities changed less drastically. However, there was a substantial modification in the dominant species composition in the climax Douglas-fir stand (site 2), which signaled functional disruptions in the whole ecosystem. Less changes occurred among dominant species in the climax western hemlock forest (site 1).

The faunistic changes in the western hemlock site were caused especially by the following dominant and constant species: *Cyclograna horrida*, *Pseudisotoma sensibilis*, *Vertagopus* sp., *Cyclograna krafti*, *Lophognathella choreutes*, *Sinella binoculata*, *Paranura colorata*, *Micrisotoma achromata*, and *Folsomia macroseta*. The first four belong to the ecomorphological group of epigeic species, the fifth to hemiedaphic and last four to euedaphic species.

The major changes in the dominant and constant species composition in the old-growth Douglas-fir forest were caused by *Xenylla humicola*, *Sphaeridia* sp.n., *Pseudisotoma sensibilis*, *Lepidocyrtus* sp. *Sinella* sp.n., and *Onychiurus flavescens*. The first four belong to epigeic, the fifth to hemiedaphic and the last one to euedaphic species.

The western hemlock site is situated on the western Pacific coast, whereas the Douglas-fir climax forest lies within Greater Victoria. The western coast of the Vancouver Island is not influenced by airborne pollutants of local origin, but may receive long-distance transported acid rain deposits from Japan and could influence life in soil (RUSEK 1993). This may explain some long-term changes in the dominance structure of the collembolan community in which representatives of all main ecomorphological groups were affected. Site 2, almost surrounded by municipalities of Victoria, and in the flight path of pollutants from Greater Seattle area, showed significant changes in the dominance structure of *Collembola*. Epigeic species were more strongly affected than hemi- and euedaphic ones. This might be explained by the influence of local industrial and traffic pollutants transported by the prevailing winds.

During long-term studies in the Tatra National Park, Slovakia, RUSEK (1993) observed extensive changes in some ecosystems and ecotones in alpine and subalpine zones caused by long-distance transported air-borne pollutants. Since 1959, he has studied *Collembola*, other soil biological parameters, soil types, soil chemical parameters, and plant communities on 25 permanent plots. Between 1977 and 1990 some startling changes occurred in many of the biotic and abiotic

parameters of the ecosystems. Many epigeic and hemiedaphic collembolan species invaded ecosystems that they had not inhabited formerly, other hemi- and euedaphic species became rare or extinct, while some formerly rare euedaphobionts became dominant. In many cases, this was caused by large amount of accumulated pollutants or pollutants transported through the most affected ecosystems by agents such as snow accumulation and water runoff gullies. In some cases, the collembolan community parameters had detected the ecological changes in advance of changes in plant communities. The same pattern is being observed in our studies on Vancouver Island.

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